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Shell Growth and Viability Differences Between the Marine Mussels *Mytilus edulis* (L.), *Mytilus galloprovincialis* (Lmk.), and Their Hybrids From Two Sympatric Populations in S.W. England

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Abstract. Mussels were collected at high and low shore locations from two *Mytilus edulis/Mytilus galloprovincialis* populations, Croyde Bay and Whitsand Bay, in S.W. England. Genotype-dependent length-at-age values were determined. At high and low shore locations at both sites, *M. edulis*-like mussels had significantly smaller length-at-age values than *M. galloprovincialis*-like and putative F1 hybrid individuals. The putative F1 hybrids exhibited length-at-age values between those of the parental types, but much closer to those of *M. galloprovincialis*-like rather than *M. edulis*-like individuals.

Genotype frequencies as a function of age were determined and relative viability coefficients estimated from comparisons of genotype frequencies of young versus old mussels. At high and low shore locations at both sites, the relative viability coefficient of *M. galloprovincialis*-like individuals was greater than that of *M. edulis*-like mussels. Putative F1 hybrids at both sites had relative viability coefficients intermediate between those of the parental types. These data indicate that the length-dependent variation in allozyme frequencies that characterizes sympatric populations can be attributed to a small but significant genotype-dependent difference in length-at-age values, but mostly to large and highly significant differences in viability.

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Introduction

Hybrid zones have been defined as "interactions between genetically distinct groups of individuals resulting in at least some offspring of mixed ancestry. Pure populations of the two genetically distinct groups are found outside of the zone of interaction" (Harrison, p. 72, 1990). As such, hybrid zones are thought to represent cases of partial (incomplete) reproductive or genetic isolation between two related species, semi-species or conspecifics. The dynamics of hybrid zones are of considerable interest from an evolutionary point of view because such zones often play important roles in models of speciation (reviewed by Hewitt, 1988).

The role of selection in the maintenance of hybrid zones has been emphasized in several reviews (Moore, 1977; Barton and Hewitt, 1985, 1989; Hewitt, 1988, 1989; Harrison, 1990). The traditional view, and the one with the most evidence to support it, is that hybrid zones are maintained by a balance between dispersal (immigration) and selection against hybrids (individuals of mixed ancestry). In this case it is more appropriate to think of hybrid zones as tension zones (Barton and Hewitt, 1985, 1989) because reduced hybrid fitness is independent of the environment. Individuals of mixed ancestry are considered to be less fit than parental types because the parental co-adapted gene complexes, which presumably evolved in response to localized selection outside the hybrid zone, are broken up by recombination within the hybrid zone. New gene combinations resulting from hybridization and recombination are considered to be less adapted to the environment (and to interaction and functioning with each other) than are the parental gene com-

plexes. Hybrids are therefore less fit and thus are selected against. Indeed, Harrison (1990) cites 20 examples of hybrid zones involving plants, insects, fish, amphibians, reptiles, birds, and mammals in which individuals of mixed ancestry have reduced fitness compared with parental types.

Moore (1977) proposed an alternative model of hybrid zone maintenance (see also Moore and Buchanan, 1985; and Moore and Koenig, 1986). This is the geographically bounded hybrid superiority model, which suggests that, within the limited environment of the hybrid zone, hybrids have a selective advantage compared to parental types when environmental factors determine relative fitness. Because the parental types are adapted to environments outside the hybrid zone, the habitat in which the hybrid zone is located is more favorable for hybrids. So far, the only evidence that supports this model comes from avian species in which adult dispersal is limited. For example, Moore and Buchanan (1985) note that their results from the Northern Flicker (woodpecker) zone are more consistent with the hybrid superiority theory than with the hybrid unfitness model. Hewitt (1988), however, suggests that the evidence does not permit this model to be distinguished from other explanations (*e.g.*, tension zones or environmental zones).

In S.W. England, sympatric populations of *Mytilus edulis* (the blue mussel) and *Mytilus galloprovincialis* (the Mediterranean mussel) exhibit a strong positive correlation between shell length and gene frequency at two allozyme loci (*Est-D* and *Odh*). Larger mussels tend to be *M. galloprovincialis*-like; that is, they possess alleles at highest frequency in pure *M. galloprovincialis* populations (Skibinski, 1983; Gardner and Skibinski, 1988). This relationship is also found in other regions of the British Isles (Skibinski and Roderick, 1991). Two hypotheses have been investigated to explain the length-dependent allozyme variation observed in hybrid populations. The first—historical change, with *M. edulis* replacing *M. galloprovincialis*—has been rejected (Gardner and Skibinski, 1988). The second—differential growth rates—was not supported by the results of transplant experiments with mussels from S.W. England (Skibinski, 1983; Skibinski and Roderick, 1989); however, *in situ* growth in sympatric mussel populations has not been studied previously. A third possibility, that differential viability causes the length-dependent allozyme variation, has also not been tested.

Investigators of the *Mytilus* contact zone in S.W. England have long thought that the hybrid zone in this area is maintained by selection, but that this selection is not principally against hybrids (Skibinski and Beardmore, 1979; Skibinski et al., 1983). Skibinski and Beardmore (1979) noted that intergradation, although extensive at many sites, is often not complete, which suggests that some genotypes of mixed ancestry have a selective advantage over *M. edulis*. The geographic distribution of sites with high genetic mixing is consistent with the hypothesis that individuals of mixed ancestry do have an advantage over at least one of the parental types in some environments (Skibinski and Beardmore, 1979; Skibinski et al., 1983). Furthermore, it was suggested that any temporal stability exhibited by the hybrid zone might result from the superior fitness of the hybrids and intergrades (Skibinski and Beardmore, 1979). In this paper, we explore these ideas further by the study of genotype-dependent viability and shell growth of mussels from two sympatric populations in S.W. England.

The objectives of our study are twofold. First, we seek to explain the length-dependent change of allozyme frequencies in sympatric populations by examining differences in genotype-dependent shell growth and viability. The use of shell-sectioning techniques permitted us to determine annual growth increments. By comparing year classes, we estimated the relative mortality of different genotypes within two hybrid populations. Second, we use the viability data to address the question of how the mussel hybrid zone is structured and maintained.

We found substantial differences in viability and small but significant differences in growth favoring *M. galloprovincialis* and individuals of mixed ancestry. The evidence suggests that these differences contribute to the variation in length-dependent allele frequency that was reported in earlier studies, and that selection against *M. edulis*-like mussels plays an important role in maintaining the hybrid zone.

Materials and Methods

In March 1987, mussels were collected at high and low shore locations from two sympatric *M. edulis*/*M. galloprovincialis* populations in S.W. England: Croyde Bay, north Devon, and Whitsand Bay, south Cornwall. These are the same locations used for previous collections (Skibinski, 1983; Gardner and Skibinski, 1988, 1990a, b). Four groups of mussels were analyzed—CHS, CLS, WHS, and WLS—where C stands for Croyde, W for Whitsand, HS for high shore, and LS for low shore. Mussels were collected from areas of the low and high shore at Croyde approximately 2.2 m and 3.5 m above chart datum (CD), and at Whitsand approximately 2.5 m and 3.8 m above CD.

In both populations, *M. edulis* numerically dominates among smaller mussels (<30 mm), whereas *M. galloprovincialis* dominates among larger mussels (>30 mm) (Skibinski, 1983; Gardner and Skibinski, 1988). Thus, it is hard to obtain small *M. galloprovincialis* and large *M. edulis*. To increase the numbers of these types of mussels for analysis, and to keep other diagnostic techniques such as starch gel electrophoresis to a minimum, large samples

of mussels were collected and sorted according to shell morphology, which is partially diagnostic for differences between *M. edulis* and *M. galloprovincialis* (Seed, 1972, 1974; Skibinski, 1983). The morphological criteria that were employed included shell height and shell curvature (both greater in *M. galloprovincialis*), the presence or absence of an anterior beak (present in *M. galloprovincialis*), and the profile of the shell (more rounded and convex in *M. galloprovincialis*).

A total of 7302 mussels with lengths of at least 20 mm were collected and sorted. For each location (CHS sample size = 1123; CLS = 1700; WHS = 2313; and WLS = 2166) the mussels were sorted into two size groups, 20–35 mm and >35 mm. Each size group was sorted according to shell morphology into three classes, "*M. edulis*-like," "*M. galloprovincialis*-like," and "intermediate." Each phenotypic group was sorted according to size into two groups, "small" and "large," a boundary size being chosen such that approximately 50% of mussels fell above and 50% below the boundary, selection being made by eye. The sorting process yielded 12 categories (two quantitative size classes × three phenotype classes × two qualitative size classes) for CLS, WHS, and WLS. Because of the limited numbers of large (>35 mm) mussels at CHS, all individuals >35 mm (n = 20) were retained as one group with no subselection. Thus, there were seven categories for CHS and twelve each for CLS, WHS, and WLS. For all four locations, 25 mussels were picked at random from each category (n = 20 for mussels >35 mm at CHS) for starch gel electrophoresis and length-at-age estimations. Table I illustrates the sorting procedure for mussels of WLS. The number of mussels subject to electrophoresis was 170 at CHS and 300 each at CLS, WHS, and WLS. Samples were either analyzed immediately or stored at −70°C for subsequent analysis.

Starch gel electrophoresis was performed on digestive gland dissected from each animal and prepared as described by Gardner and Skibinski (1988). Two allozyme loci, esterase-D (EST-D; EC 3.1.1.1) and octopine dehydrogenase (ODH; EC 1.5.1.11) were assayed, because these two loci show large allele frequency differences between *M. edulis* and *M. galloprovincialis* (Skibinski, 1983; Sanjuan *et al.*, 1990). To aid in data analysis, the compound allele system described by Skibinski (1983) was used. At a given locus, the compound *E* allele is obtained by pooling those alleles that are at highest frequency in "pure" *M. edulis*, and the compound *G* allele is obtained by pooling those alleles that are at highest frequency in "pure" *M. galloprovincialis*. Thus, for two polymorphic loci such as *Est-D* and *Odh*, there are nine dilocus genotype combinations ranging from the most *M. edulis*-like (*E/E E/E*), through the intermediate or putative F1 hybrid (*E/G E/G*) to the most *M. galloprovincialis*-like (*G/G G/G*). For the rest of the paper, the terms *galloprovincialis*, *edulis*, and hybrid refer to *M. galloprovincialis*-like (*G/G G/G*), *M. edulis*-like (*E/E E/E*), and putative F1 hybrid (*E/G E/G*) individuals of sympatric populations, without implying that these are truly pure types, but with the understanding that distinctive phenotype differences exist between the groups (*e.g.*, Skibinski *et al.*, 1978a, b; Beaumont *et al.*, 1989).

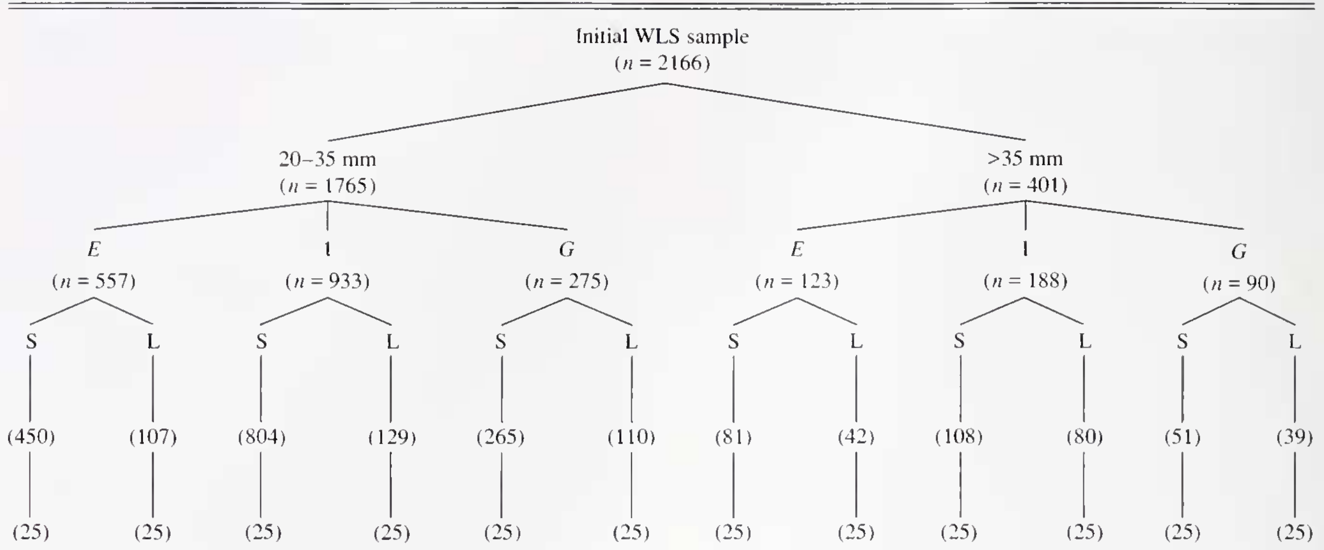
We focused upon only three (*E/E E/E*, *E/G E/G* and *G/G G/G*) of the nine genotypes because these represent the two extremes (both parental genotypes) and the intermediate (putative F1 hybrid), and consequently growth and viability differences between these groups are likely to be as great as any that occur within the zone of sympatry. Furthermore, these three genotypes represent between 65 and 70% of the total number of individuals within each population, making them of considerable importance in numerical terms alone. This does not imply that the other six genotypes are unimportant or occur at such low frequency that they are insignificant, but simply reflects the advantage of working with genotypes that are well represented in both populations and have arguably the most potential (at least initially) to provide data on fitness differences within the zone of sympatry. Obviously, the ability to differentiate between *edulis*, *galloprovincialis*, and hybrid individuals is important in identifying growth and viability differences between these types. However, because of introgression in these populations (*e.g.*, Skibinski, 1983; Skibinski *et al.*, 1983; Gardner and Skibinski, 1988), pure individuals or genuine F1 hybrids might not exist, and thus would not be detectable, regardless of the number of genetic markers used.

The allozymes selected provide a strong indication of background genotype in mussels from sympatric populations. For example, *G/G G/G* individuals from sympatric populations are morphologically and electrophoretically very similar to *M. galloprovincialis* from pure allopatric populations, just as *E/E E/E* individuals from sympatric populations most closely resemble *M. edulis* from pure allopatric populations (*e.g.*, Grant and Cherry, 1985; Sanjuan *et al.*, 1990).

Shell lengths (±0.1 mm) of all mussels typed by electrophoresis were recorded. Shells were sectioned to establish that age determination from external check marks could be performed accurately. A valve from each of 155 randomly chosen individuals from all four locations was thin-sectioned, and an acetate peel replica was prepared (*e.g.*, Lutz, 1976; Richardson *et al.*, 1979). The number of internal annual growth bands was counted, and the distance from the umbo to each mark was measured to provide length-at-age data. The processes of counting the annual bands from the acetate peels and from the exterior of the valve were carried out independently to minimize bias in the results. When a peel or the valve from which it was derived could not be scored with total confidence,

Table I

The sorting procedure used to obtain 12 groups of 25 mussels each (where possible) for analysis, as exemplified by the Whitsand low shore (WLS) sample



E = *edulis* mussels; I = intermediate mussels; *G* = *galloprovincialis* mussels; S = small; L = large.

the data pair was discarded (there was no evidence of a nonrandom factor explaining which data pairs could or could not be accurately scored). Nine of 65 mussels were incorrectly aged, eight by ±1 year, and one by 2 years. Regression analysis of the number of annual growth rings from the acetate peel against the number estimated from the valve exterior was carried out, the two being highly correlated ($R^2 = 0.908$; $n = 65$; $P < 0.001$).

The ages of all remaining nonsectioned mussels were determined by examination of external growth marks. Each mussel provided length-at-age data for a minimum of 4 years of age up to a maximum of 13 years of age, with an average of about 6–7 years. Data were analyzed by univariate ANOVA of each length-at-age category. This analysis is based on minimal assumptions, the results are easily interpretable and biologically meaningful, and maximum information can be extracted from the data set because a large proportion of the values can be used. This is a conservative approach, so that if significant length-at-age differences are observed it can be assumed that they represent genuine differences. A slight loss of statistical power is associated with this approach, but this is offset by the advantages described above. To control for the multiple testing involved with this approach, we used the Bonferroni test, which compensates for the increased probability of Type I error rate (the sequential Bonferroni test, which is less conservative than the standard Bonferroni test [Rice, 1989], gave identical results). With the Bonferroni procedure, the alpha level (nominally alpha = 0.05) is divided by the total number of tests made of the same hypothesis, which at CHS, WHS, and WLS was 10 each, giving an acceptance value of alpha = 0.005 at these locations; and at CLS was 8, giving an acceptance value of alpha = 0.00625 at this location. We employed the univariate option of the PROC GLM (General Linear Model) subroutine of SAS (SAS Institute, 1987) with the Ryan-Einot-Gabriel-Welsch multiple range test (REGWQ option) to locate between-subject effects. The REGWQ multiple range test is particularly appropriate because it controls the experimentwise Type I error rate (Day and Quinn, 1989). The data were tested for normality using the Shapiro-Wilkes statistic: transformations were unnecessary because the data were normally distributed.

Best-fit growth curves were derived from polynomial regression computed by the PROC GLM procedure of SAS (*e.g.*, MacDonald and Thompson, 1985, 1988), which has an advantage over the von Bertalanffy function in that it does not impose asymptotic behaviour (Roff, 1980; MacDonald and Thompson, 1985). A cubic polynomial best explained variation in the growth curves following stepwise significance testing of each newly added term (*e.g.*, Sokal and Rohlf, 1981, p. 673).

Following electrophoresis and age determination, data from the mussels of the four locations were tabulated according to age and dilocus genotype to permit estimation of age-dependent genotype frequencies. An example is given in Table II. The predicted frequency of each genotype of any age in the initial random sample was estimated, taking into account, and adjusting for, the sorting procedure described above. For example, using the data

Table II

The method used to estimate genotype frequencies as exemplified by data from Whitsand low shore (WLS)

	20–35 mm category (n = 1765 mussels collected)			>35 mm category (n = 401 mussels collected)		
	Dilocus genotype					
	E/E E/E	*E/G E/G*	*G/G G/G*	*E/E E/E*	*E/G E/G*	*G/G G/G*
Age (yr)						
0	32	3	1			
1	27	6	3			
2	21	10	8			
3	9	13	17	5	10	19
4				2	12	20
5				1	18	28
6				0	8	14
7				1	4	7
Subtotal	89	32	29	9	52	88
Total		150			149	

E/E E/E = *edulis* mussels; *E/G E/G* = putative F1 mussels; *G/G G/G* = *galloprovincialis* mussels.

from Table II, the predicted frequency of 3-year-old *G/G G/G* mussels among all 3-year-old mussels in the WLS sample is

$$\frac{((17 \times 1765/150) + (19 \times 401/149))}{((9 + 13 + 17) \times (1765/150) + (5 + 10 + 19) \times (401/149))} = 0.456$$

In the above equation, the numerator estimates the number of 3-year-old *G/G G/G* mussels in the 1765 + 401 total, and the denominator estimates the total number of 3-year-old mussels of all genotypes in the same total.

Results

The results of the ANOVA for the high and low shore locations at Croyde are given in Table III, and for the two locations at Whitsand in Table IV. Data are presented for mussels up to the maximum age at which all three genotypes co-occur. Thus, although data were available for certain genotypes up to length-at-age 13 years, these were not included if the same data were not available for any other genotype. All four locations have a similar pattern of between-subject (genotype) effects throughout the analyses. Among the youngest individuals of the three genotypes, length-at-age values are not significantly different, but at age 4 years and older significant differences are apparent. Nonsignificant differences between the genotypes among the oldest age classes may be partially attributable to the small sample sizes for these oldest mussels. Where significant between-subject effects exist at CHS, CLS, and WLS, the *E/G E/G* and *G/G G/G* genotypes exhibit nonsignificant length-at-age differences throughout their life spans, whereas the *E/E E/E* mussels have statistically lower mean length-at-age values than both these genotypes. Where significant between-subject effects exist at WHS, the *G/G G/G* mussels have significantly greater mean length-at-age values than the *E/G E/G* individuals (at ages 7, 8, and 9 years). From age 3 years onwards, one or, more usually, both of the *E/G E/G* and *G/G G/G* genotypes have significantly greater length-at-age values than the *E/E E/E* mussels. The maximum difference in length-at-age values between the three genotypes (*i.e.*, maximum minus minimum value regardless of genotype) is also presented in each table. Length-at-age differences among older individuals are smaller than those observed among intermediate-aged mussels, which suggests that, on average, individuals that live the longest, regardless of genotype, have similar length-at-age values. Thus, among the *edulis* mussels, individuals that exhibit greatest maximum longevities also exhibit greatest length-at-age values at all ages.

Growth curves fitted by polynomial regression (Fig. 1) are very similar between genotypes for mussels of less than 4 years of age, but diverge thereafter. The standardized polynomial partial regression coefficients (up to the cubic term) for each growth line and the R^2 values, which give an indication of how well each line fits the observed data, are given in Table V.

High or low shore location within a site has a pronounced effect upon growth (comparisons of growth were based upon tests of differences in the linear parameter of the cubic regression models). At Croyde, the three genotypes all have greater length-at-age values in the low shore than in the high shore; this difference is nonsignificant for

Table III

Analysis of variance, with significant Ryan-Einot-Gabriel-Welsch multiple range test results, of mean length-at-age data for mussels from Croyde high and low shore

Age (yr)	*E/E E/E* mean length (mm)	*E/G E/G* mean length (mm)	*G/G G/G* mean length (mm)	Max. diff. (mm)	*N*	*P*	REGWQ
CHS							
1	5.58	5.67	5.59	0.09	94	0.9720^{NS}	
2	10.08	10.83	10.46	0.75	94	0.4011^{NS}	
3	15.25	16.23	15.76	0.98	94	0.3910^{NS}	
4	19.62	20.99	20.97	1.79	94	0.0707^{NS}	
5	22.75	25.00	25.33	2.58	87	0.0013*	*G/G = E/G > E/E*
6	24.64	28.16	28.55	3.91	72	0.0001*	*G/G = E/G > E/E*
7	25.63	31.68	30.91	6.05	47	0.0001*	*E/G = G/G > E/E*
8	26.36	34.10	32.78	7.74	30	0.0001*	*E/G = G/G > E/E*
9	29.03	35.53	33.40	6.50	19	0.0013*	*E/G = G/G > E/E*
10	30.15	36.73	33.20	6.58	11	0.0312^{NS}	
CLS							
1	6.54	6.78	6.74	0.24	130	0.6721^{NS}	
2	13.44	13.02	13.28	0.42	130	0.7986^{NS}	
3	20.72	20.48	20.95	0.23	130	0.8065^{NS}	
4	25.45	27.23	26.73	1.78	127	0.0034*	*E/G = G/G > E/E*
5	29.41	31.08	30.96	1.67	108	0.0038*	*G/G > E/E*
6	32.86	34.60	34.34	1.74	88	0.0127^{NS}	
7	35.70	36.09	36.28	0.58	62	0.9110^{NS}	
8	37.76	38.70	39.22	1.46	37	0.5803^{NS}	

N = number of individuals; *P* = significance level following Bonferroni test; NS = nonsignificant following Bonferroni test; * = significant following Bonferroni test at alpha = 0.05/k (where k = number of tests); REGWQ = Ryan-Einot-Gabriel-Welsch multiple range test results; CHS = Croyde high shore; CLS = Croyde low shore; *E/E E/E, E/E* = *edulis* mussels; *E/G E/G, E/G* = putative F1 mussels; *G/G G/G, G/G* = *galloprovincialis* mussels.

the *E/G E/G* genotype only (CHS *vs.* CLS: *E/E E/E*, $t = 13.951$, df = 129, $P < 0.001$; *E/G E/G*, $t = 3.290$, df = 22, $P > 0.05^{NS}$; *G/G G/G*, $t = 10.484$, df = 65, $P < 0.001$: all significance levels given in this paragraph were determined after Bonferroni test; *i.e.*, if $P = 0.05/14 = 0.00357$ or less, the result is significant). Even the greatest length-at-age values at CHS (the *E/G E/G* genotype) are less than the greatest length-at-age values (the *E/E E/E* genotype) at CLS (CHS *E/G E/G vs.* CLS *E/E E/E*: $t = 17.826$, df = 74, $P < 0.001$). At Whitsand, each genotype has greater length-at-age values in the low shore than in the high shore; this difference is nonsignificant only for the putative F1 hybrids (WHS *vs.* WLS: *E/E E/E*, $t = -9.502$, df = 144, $P < 0.001$; *E/G E/G*, $t = 1.229$, df = 46, $P > 0.05^{NS}$; *G/G G/G*, $t = -3.405$, df = 32, $P < 0.002$). The greatest length-at-age values at WHS (the *G/G G/G* genotype) are less than the greatest length-at-age values (the *E/E E/E* genotype) at WLS, although WHS *G/G G/G* length-at-age values are slightly lower at ages < 4 years and slightly greater at ages > 4 years than WLS *E/E E/E* values (WHS *G/G G/G* vs WLS *E/E E/E*, $t = 6.604$, df = 100, $P < 0.001$). Comparison of length-at-age data between the site locations indicates that values at WHS and at WLS are greater than those at CHS and at CLS respectively (CHS *vs.* WHS: *E/E E/E*, $t = 4.399$, df = 127, $P < 0.001$; *E/G E/G*, $t = 4.292$, df = 25, $P > 0.05^{NS}$; *G/G G/G*, $t = 0.416$, df = 32, $P > 0.05^{NS}$; CLS *vs.* WLS: *E/E E/E*, $t = 4.779$, df = 146, $P < 0.001$; *E/G E/G*, $t = 0.513$, df = 43, $P > 0.05^{NS}$; *G/G G/G*, $t = 4.059$, df = 65, $P < 0.001$). Thus, as reported for other *Mytilus* populations (*e.g.*, Dickie *et al.*, 1984; Mallet *et al.*, 1987), site explains as much, if not more, of the variation in growth as is explained by genotype.

At all locations, genotype frequency as a function of age describes a sigmoidal pattern (Tables VI and VII). The frequency of *edulis* is highest among the youngest mussels, whereas the hybrids and *galloprovincialis* both occur at very low frequencies. With increasing age, the frequency of *edulis* decreases, whereas the frequencies of hybrids and *galloprovincialis* increase. Regression analysis of arcsine squareroot transformed compound *E* allele frequency (to transform a sigmoidal to a linear relationship, Sokal and Rohlf, 1981) as a function of age describes a negative linear relationship that is significant at CHS ($R^2 = 0.869$, $n = 8$, $P < 0.001$), CLS ($R^2 = 0.966$, $n = 8$, $P < 0.001$), WHS ($R^2 = 0.823$, $n = 8$, $P < 0.001$) and WLS ($R^2 = 0.736$, $n = 9$, $P < 0.01$) (Figs. 2 and 3). The mean slope of the equation for Croyde mussels is not signifi-

Table IV

Analysis of variance, with significant Ryan-Einot-Gabriel-Welsch multiple range test results, of mean length-at-age data for mussels from Whitsand high and low shore

Age (yr)	*E/E E/E* mean length (mm)	*E/G E/G* mean length (mm)	*G/G G/G* mean length (mm)	Max. diff. (mm)	*N*	*P*	REGWQ
WHS							
1	6.18	6.22	6.23	0.05	98	0.9913^{NS}	
2	10.99	11.91	11.69	0.92	98	0.2429^{NS}	
3	16.01	18.07	17.49	2.06	98	0.0149^{NS}	
4	20.63	23.49	23.61	2.98	98	0.0002*	*G/G* = *E/G* > *E/E*
5	24.08	28.38	29.36	5.28	97	0.0001*	*G/G* = *E/G* > *E/E*
6	27.02	31.85	33.97	6.97	88	0.0001*	*G/G* = *E/G* > *E/E*
7	29.85	34.48	37.92	8.07	60	0.0001*	*G/G* > *E/G* > *E/E*
8	34.18	36.19	40.39	6.21	35	0.0001*	*G/G* > *E/G* = *E/E*
9	35.72	38.60	42.18	6.46	25	0.0043*	*G/G* > *E/G* = *E/E*
10	40.15	40.02	44.40	4.38	12	0.2051^{NS}	
WLS							
1	7.08	6.94	6.47	0.61	129	0.4947^{NS}	
2	13.25	13.48	13.65	0.40	129	0.8193^{NS}	
3	19.32	20.12	20.71	1.39	129	0.2092^{NS}	
4	24.67	26.57	27.21	2.54	129	0.0136^{NS}	
5	28.50	32.26	33.95	5.45	116	0.0001*	*G/G* = *E/G* > *E/E*
6	31.93	36.75	38.51	6.58	90	0.0001*	*G/G* = *E/G* > *E/E*
7	33.61	39.99	42.32	8.71	67	0.0001*	*G/G* = *E/G* > *E/E*
8	35.80	43.28	45.27	9.47	35	0.0015*	*G/G* = *E/G* > *E/E*
9	39.00	44.74	45.94	6.94	19	0.2817^{NS}	
10	45.30	46.67	49.50	4.20	10	0.5705^{NS}	

N = number of individuals; *P* = significance level following Bonferroni test; NS = nonsignificant following Bonferroni test; * = significant following Bonferroni test at alpha = 0.05/k (where k = number of tests); REGWQ = Ryan-Einot-Gabriel-Welsch multiple range test results; WHS = Whitsand high shore; WLS = Whitsand low shore; *E/E E/E*, *E/E* = *edulis* mussels; *E/G E/G*, *E/G* = putative F1 mussels; *G/G G/G*, *G/G* = *galloprovincialis* mussels.

cantly different from that for Whitsand mussels (mean ± SD of −10.842 ± 4.343, n = 2, at Croyde; −9.246 ± 0.771, n = 2, at Whitsand; t = −0.210, df = 33, $P > 0.05$).

A relative viability coefficient for each genotype (Table VIII) was calculated from the data in Tables VI and VII. A genotype frequency estimate among young mussels (GF_{young}) was obtained from the mean genotype frequency of the first three years for which data were available. For example, for *E/E E/E* mussels of CHS, this value is the mean of the frequency values for individuals of ages 4, 5, and 6 years (*i.e.*, [0.93 + 0.97 + 0.97]/3 = 0.957) shown in Table VII. For *E/G E/G* mussels of CLS, the value is the mean genotype frequency of individuals of ages 3, 4, and 5 years (*i.e.*, [0 + 0 + 0.08]/3 = 0.027) shown in Table VII. Similarly, the genotype frequency among the oldest individuals (GF_{old}) was calculated as the mean for the last three years for which data were available. For example, for all genotypes at CHS, this is the mean frequency of 9, 10, and 11 years of age; for all genotypes at CLS, it is the mean frequency of 8, 9, and 10 years of age. Mean gene frequencies were calculated to reduce the problem of small sample sizes among the youngest and oldest mussels. Comparison of gene frequencies estimated in this way could lead to conservative estimates of viability compared with values obtained using the youngest and oldest individuals owing to the pooling of data from three year classes. However, the greatest rate of change in genotype frequencies occurs among mussels of intermediate ages and not among the oldest or youngest mussels used for this calculation. In each case, an absolute viability coefficient was obtained by dividing GF_{old} by GF_{young}. Relative viability coefficients were obtained by dividing each absolute viability coefficient by the highest observed value of all absolute viability coefficients among the three genotypes to give one relative viability coefficient value of 1.000 and two others as proportions of 1.000. The relative viability coefficients calculated in this way should not be confused with coefficients estimated for the interval from zygote to reproductive maturity, but they nevertheless give some indication of relative viability and mortality during much of adult life. At all four locations, the relative viability coefficient of *galloprovincialis* is much higher than that of *edulis* (Table VIII).

Discussion

In S.W. England, *M. galloprovincialis* is presumed to be at the northernmost limit of its distribution (Seed, 1971; Gosling, 1984). For sites in England, it may therefore be predicted that the endemic cold-water *M. edulis* form should have a growth advantage over the warm-water *M. galloprovincialis* form. At <20°C in the laboratory, Seed (1971) found that *M. edulis* grew up to four times faster than *M. galloprovincialis* from Rock, S.W. England. However, he was doubtful if these differences would be maintained under natural conditions. Using a larger data set taken from mussels that, since their settlement, had been growing at high and low shore locations in two hybrid populations in S.W. England, we have shown that *galloprovincialis* has a small but significant growth advantage over *edulis*.

The negative correlation between *E* allele frequency and age lends support to the third hypothesis, advanced by Skibinski (1983), that differential mortality acts against the more numerous and smaller *edulis*. The most pronounced changes in length-dependent allele frequencies occur at older ages (8–9 years at CHS and WHS, 6–8

Table V

Parameters of the polynomial regressions for genotype-dependent best-fit growth curves

Location	Genotype	Intercept	Linear term	Square term (×10)	Cubic term (×10)	R^2
CHS	*E/E E/E*	−1.842	7.590	−6.697	0.228	0.898
	E/G E/G	−0.293	6.041	−1.647	−0.069	0.947
	G/G G/G	−1.708	7.064	−3.485	0.002	0.944
CLS	*E/E E/E*	−3.102	10.350	−9.716	0.410	0.953
	E/G E/G	−1.151	7.632	0.014	−0.462	0.951
	G/G G/G	−3.074	10.138	−7.913	0.235	0.956
WHS	*E/E E/E*	−0.146	6.554	−4.319	0.169	0.896
	E/G E/G	−2.301	8.528	−5.768	0.152	0.920
	G/G G/G	−1.062	6.866	−1.165	−0.113	0.943
WLS	*E/E E/E*	−1.648	9.161	−7.914	0.311	0.866
	E/G E/G	−1.016	7.890	−2.154	−0.097	0.921
	G/G G/G	−2.344	8.796	−3.449	−0.032	0.934

CHS, CLS = Croyde high shore, Croyde low shore; WHS, WLS = Whitsand high shore, Whitsand low shore; *E/E E/E* = *edulis* mussels; *E/G E/G* = putative F1 mussels; *G/G G/G* = *galloprovincialis* mussels; R^2 = coefficient of determination.

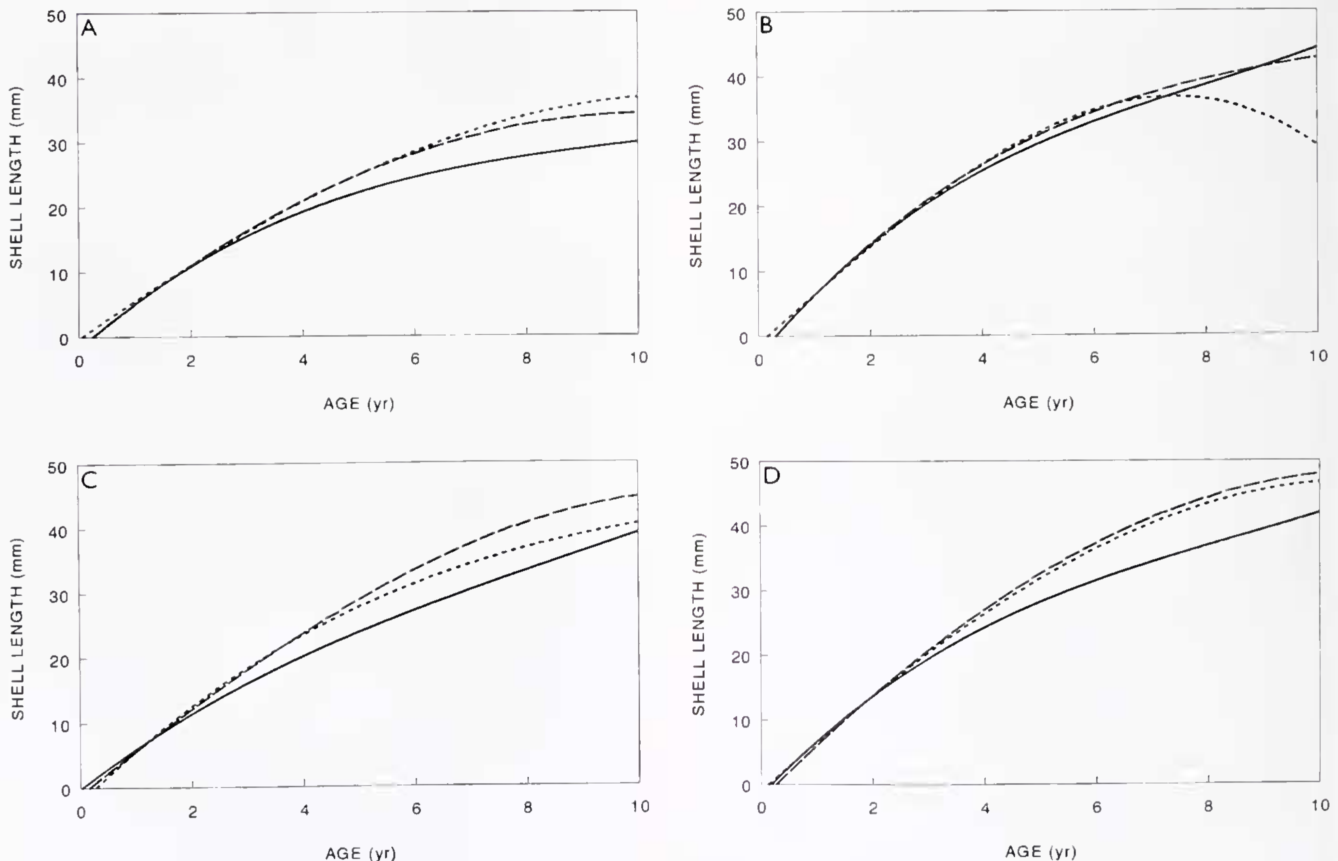


Figure 1. Best-fit polynomial growth curves for *edulis* (*E/E E/E*) (solid line), F1 hybrid (*E/G E/G*) (dotted line), and *galloprovincialis* (*G/G G/G*) (broken line) mussels, at (A) Croyde high shore, (B) Croyde low shore, (C) Whitsand high shore, and (D) Whitsand low shore.

Table VI

Predicted genotype frequencies as a function of age (calculated from electrophoretic and external annual shell check mark data) for mussels from Croyde (see Table II for further explanation)

Age (yr)	CHS				CLS			
	E/E E/E	*E/G E/G*	*G/G G/G*	*N*	*E/E E/E*	*E/G E/G*	*G/G G/G*	*N*
3	—	—	—		1.00	0	0	3
4	0.93	0	0.07	7	1.00	0	0	19
5	0.97	0.03	0	14	0.90	0.08	0.02	20
6	0.97	0.02	0.01	25	0.82	0.03	0.15	26
7	0.73	0.16	0.11	17	0.29	0.29	0.42	25
8	0.74	0.19	0.07	11	0.27	0.08	0.65	15
9	0.37	0	0.63	9	0.05	0	0.94	14
10	0.47	0.53	0	6	0	0	1.00	8
11	0.19	0	0.81	4	—	—	—	
Total				93				130

CHS, CLS = Croyde high shore, Croyde low shore; *E/E E/E* = *edulis* mussels; *E/G E/G* = putative F1 mussels; *G/G G/G* = *galloprovincialis* mussels; *N* = number of mussels.

years at CLS and at WLS; Tables VI and VII), whereas the most pronounced differences in length-at-age values occur earlier (significant differences exist by 4 years of age at CLS and WHS, and by 5 years at CHS and WLS). Differential growth therefore begins several years before the greatest differences in genotype frequencies are generated, so that differential growth cannot be solely responsible for the length-dependent changes in allele frequencies. Thus, small but significant differences in length-at-age values are insufficient by themselves to explain the pronounced decrease in compound *E* allele frequency, even though the growth differences must contribute (slightly) to this phenomenon.

Significant differences in length-at-age values are observed at age 4 years and older and among intermediate-aged, but not the very oldest, mussels. This can be partially explained by the small sample sizes of the oldest mussels, but examination of the maximum difference in length-at-age indicates that this parameter increases with age, reaches its greatest values at intermediate ages, and then decreases among the oldest age classes. A threefold explanation for this can be advanced. First, up to about 4 years of age, length-at-age values are not significantly different between the genotypes, and viability differences are small (*e.g.*, Gardner and Skibinski, 1988; Figs. 2 and 3 of the present paper). Second, at intermediate ages, signifi-

Table VII

Predicted genotype frequencies as a function of age (calculated from electrophoretic and external annual shell check mark data) for mussels from Whitsand (see Table II for further explanation)

Age (yr)	WHS				WLS			
	E/E E/E	*E/G E/G*	*G/G G/G*	*N*	*E/E E/E*	*E/G E/G*	*G/G G/G*	*N*
3	—	—	—	—	1.00	0	0	4
4	1.00	0	0	1	0.65	0.35	0	8
5	1.00	0	0	9	0.98	0	0.02	26
6	0.96	0.04	0	28	0.84	0.14	0.02	23
7	0.73	0.10	0.17	25	0.72	0.25	0.03	29
8	0.72	0.18	0.10	10	0.47	0.42	0.11	18
9	0.33	0.16	0.51	13	0.15	0.25	0.60	9
10	0.33	0.33	0.34	3	0	0.56	0.44	7
11	0	0.58	0.42	4	0.33	0.67	0	3
12	0.49	0.28	0.23	3	—	—	—	—
13	0	0.56	0.44	2	—	—	—	—
Total				98				127

WHS, WLS = Whitsand high shore, Whitsand low shore; *E/E E/E* = *edulis* mussels; *E/G E/G* = putative F1 mussels; *G/G G/G* = *galloprovincialis* mussels; *N* = number of mussels.

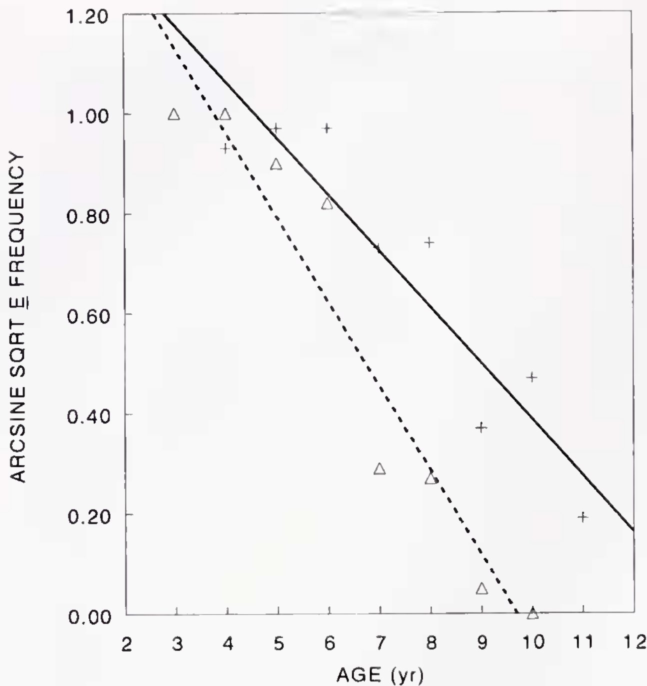


Figure 2. Arcsine square root compound *E* allele frequency as a function of age at Croyde high shore (+ and solid line) and Croyde low shore (△ and broken line).

Based on genotype frequency differences between young and old mussels, relative viability coefficients were calculated that demonstrate a high selective mortality against *edulis*. Increasingly more evidence points to the conclusion that strong selection is common in natural populations (Endler, 1986), and that selection coefficients in hybrid zones can also be very large (*e.g.*, Dowling and Moore, 1985; Barton and Hewitt, 1985; Hewitt, 1988). The relative viability coefficients estimated in this study indicate that selection against *edulis* is indeed strong—at all four locations *edulis* had viability coefficients that are orders of magnitude smaller than those of *galloprovincialis*. The extent of the coefficient differences between *edulis* and *galloprovincialis* is strong support for the hypothesis of differential viability (Skibinski, 1983) as an explanation for the pattern of length-dependent allele frequencies.

Mussels reproduce by external fertilization, producing pelagic larvae that are almost all immigrants at the time of settlement (Tracey et al., 1975). Because components of fitness such as viability and fecundity are much lower in *edulis* than in *galloprovincialis*, considerable immigration of *edulis* spat is required to maintain the genetic structure of these populations, which are characterized by a very high frequency of *edulis* among the smallest and youngest mussels (Skibinski, 1983; Gardner and Skibinski, 1988). Furthermore, this genetic structure is apparently stable in the short term (over a period of 6 years), an

cant length-at-age differences exist between the genotypes. It is at this stage that viability differences between the genotypes are most pronounced, resulting in greatest differential mortality of *edulis* mussels. Third, following this period of maximum differential mortality, the oldest surviving mussels exhibit nonsignificant differences in length-at-age values. Thus, during the second stage, the highest mortality rates are experienced by the *edulis* individuals with the lowest viabilities (and also the smallest length-at-age values), resulting in the significant differences in mean length-at-age values observed at this time. The *edulis* with (by definition) the highest viabilities (and the greatest length-at-age values) survive this period so that among the oldest age classes, when viability differences are once again less pronounced, there are no significant differences in length-at-age values. The positive association between length-at-age values and viability among the *edulis* individuals can be explained in one of two ways. One, the association is noncausal, resulting from, for example, pleiotropy (*e.g.*, Falconer, 1989). Two, it is causal, and occurs because increased shell length offers a refuge from predators (Gardner and Skibinski, 1991) and confers a fitness advantage in terms of increased byssal strength of attachment to the substrate, which decreases the chance of being dislodged from the rock face and swept out to sea (Gardner and Skibinski, 1991; Willis and Skibinski, 1992).

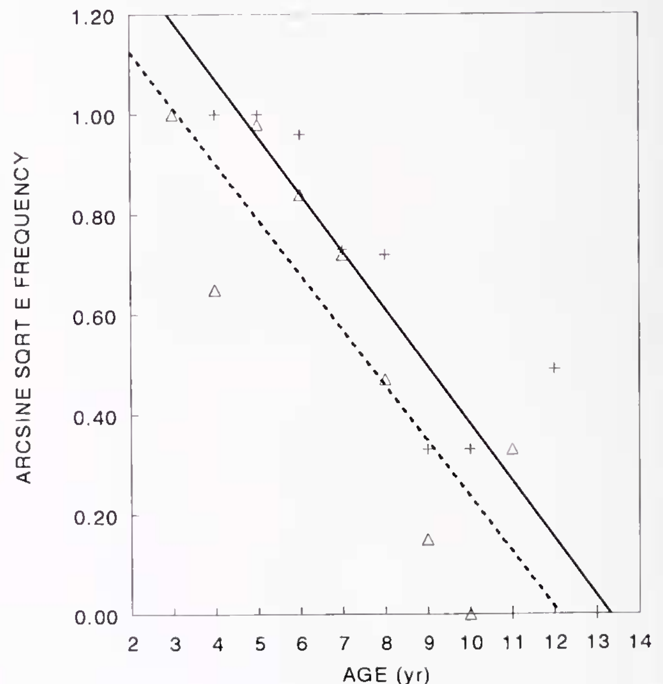


Figure 3. Arcsine square root compound *E* allele frequency as a function of age at Whitsand high shore (+ and solid line) and Whitsand low shore (△ and broken line).

Table VIII

Genotype-dependent relative viability coefficients for high and low shore locations at Croyde and Whitsand, calculated from the data of age-dependent variation given in Tables VII and VIII

	CHS			CLS		
	E/E E/E	*E/G E/G*	*G/G G/G*	*E/E E/E*	*E/G E/G*	*G/G G/G*
GF_{young}	0.957	0.017	0.027	0.967	0.027	0.007
GF_{old}	0.343	0.177	0.480	0.107	0.027	0.863
Absolute viability	0.358	10.412	17.778	0.111	1.000	123.286
Relative viability	0.020	0.586	1.000	0.001	0.008	1.000
	WHS			WLS		
	E/E E/E	*E/G E/G*	*G/G G/G*	*E/E E/E*	*E/G E/G*	*G/G G/G*
GF_{young}	0.987	0.013	0.001*	0.877	0.117	0.007
GF_{old}	0.163	0.473	0.363	0.160	0.493	0.347
Absolute viability	0.165	36.385	363.000	0.182	4.213	49.571
Relative viability	0.0005	0.100	1.000	0.004	0.085	1.000

CLS, CHS = Croyde low shore, Croyde high shore; WLS, WHS = Whitsand low shore, Whitsand high shore; *E/E E/E* = *edulis* mussels; *E/G E/G* = putative F1 mussels; *G/G G/G* = *galloprovincialis* mussels; GF_{young}, GF_{old} = gene frequencies among the young and old mussels; * = actual mean value of zero, assumed value of 0.001.

interval representing a minimum 50% turnover in population numbers (Gardner and Skibinski, 1988). Thus our data (Gardner and Skibinski, 1988, 1990a, and this paper) indicate that these sympatric *Mytilus* populations in S.W. England are maintained by a balance between the differential viability acting against *edulis* and the predominance of *edulis* spat among immigrants. One reason for a very low proportion of *galloprovincialis* spat, despite their pronounced viability advantage over *edulis*, is that *M. galloprovincialis* reaches its northernmost limit in S.W. England and is apparently restricted from successfully settling further north by the lower seawater temperatures. This is indeed the case for most other warm-water Mediterranean forms that extend this far north (Yonge, 1949).

The mechanism responsible for greater *edulis* mortality is thought to involve genotype-dependent differences in strength of attachment of the byssus (Gardner and Skibinski, 1991; Willis and Skibinski, 1992). At both Croyde and Whitsand, at all shell lengths, *edulis* are more easily removed from the substrate than *galloprovincialis* of the same length. This results in part from morphological differences between the two mussel types and is consistent with evolutionary trends observed in lineages of byssally attached bivalves (Yonge and Campbell, 1968). Differences attributable to wave exposure have been reported in the ecological distributions of the two mussel types in S.W. England (Skibinski, 1983; Gardner and Skibinski, 1988), the Atlantic coast of France (Seed, 1972), and southern Ireland (Gosling and Wilkins, 1981) where *galloprovincialis* frequency is positively correlated with increasing wave exposure. At the microgeographic level among sympatric populations in S.W. England, *galloprovincialis* frequency is greatest in the high shore and least in the low shore; this distribution is significantly correlated with site-specific variability in wave action (Skibinski, 1983; Gardner and Skibinski, 1988). Thus, differences in strength of attachment between the two species are consistent with the relationship between wave exposure and the ecological distribution of the two mussel types (Gardner and Skibinski, 1991).

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Literature Cited

Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.* **16:** 113–148.

Barton, N. H., and G. M. Hewitt. 1989. Adaptation, speciation and hybrid zones. *Nature* **341:** 497–503.

Beaumont, A. R., R. Seed, and P. Garcia-Martinez. 1989. Electrophoretic and morphometric criteria for the identification of the mussels *Mytilus edulis* and *M. galloprovincialis*. Pp. 251–258 in *Reproduction, Genetics and Distributions of Marine Organisms*, J. S. Ryland and P. A. Tyler, eds. Proc. 23rd European Marine Biology Symposium, University of Wales, Swansea. Olsen and Olsen, Fredensborg, Denmark.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* **59:** 433–463.

Dickie, L. M., P. R. Boudreau, and K. R. Freeman. 1984. Influences of stock and site on growth and mortality in the blue mussel (*Mytilus edulis*). *Can. J. Fish. Aquat. Sci.* **41:** 134–140.

Dowling, T. E., and W. S. Moore. 1985. Evidence for selection against hybrids in the Family Cyprinidae (Genus *Notropis*). *Evolution* **39:** 152–158.

Endler, J. A. 1986. Natural selection in the wild. *Monographs in Population Biology*, 21. Princeton University Press, Princeton, NJ.

Falconer, D. S. 1989. *Introduction to Quantitative Genetics.* 3rd ed. Longman Scientific and Technical, Harlow, England.

Gardner, J. P. A., and D. O. F. Skibinski. 1988. Historical and size-dependent genetic variation in hybrid mussel populations. *Heredity* **61:** 93–105.

Gardner, J. P. A., and D. O. F. Skibinski. 1990a. Genotype-dependent fecundity and temporal variation of spawning in hybrid mussel (*Mytilus*) populations. *Mar. Biol.* **105:** 153–162.

Gardner, J. P. A., and D. O. F. Skibinski. 1990b. Thermostability differences of allozyme loci in *Mytilus edulis*, *M. galloprovincialis* and hybrid mussels. *Mar. Ecol. Prog. Ser.* **64:** 99–105.

Gardner, J. P. A., and D. O. F. Skibinski. 1991. Biological and physical factors influencing genotype-dependent mortality in hybrid mussel populations. *Mar. Ecol. Prog. Ser.* **71:** 235–243.

Gosling, E. M. 1984. The systematic status of *Mytilus galloprovincialis* in western Europe: a review. *Malacologia* **25:** 551–568.

Gosling, E. M., and N. P. Wilkins. 1981. Ecological genetics of the mussels *Mytilus edulis* and *Mytilus galloprovincialis* on Irish coasts. *Mar. Ecol. Prog. Ser.* **4:** 221–227.

Grant, W. S., and M. I. Cherry. 1985. *Mytilus galloprovincialis* Lmk. in Southern Africa. *J. Exp. Mar. Biol. Ecol.* **90:** 179–191.

Harrison, R. G. 1990. Hybrid zones: windows on evolutionary process. *Oxf. Surv. Evol. Biol.* **7:** 69–128.

Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. *Trends Ecol. Evol.* **3:** 158–167.

Hewitt, G. M. 1989. The subdivision of species by hybrid zones. Pp 85–110 in *Speciation and Its Consequences*, D. Otte and J. Endler, eds. Sinauer Associates, Sunderland, MA.

Lutz, R. A. 1976. Annual growth patterns in the inner shell of *Mytilus edulis*. *J. Mar. Biol. Ass. U.K.* **56:** 723–731.

MacDonald, B. A., and R. J. Thompson. 1985. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. I. Growth rates of shell and somatic tissue. *Mar. Ecol. Prog. Ser.* **25:** 279–294.

MacDonald, B. A., and R. J. Thompson. 1988. Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the giant scallop *Placopecten magellanicus*. *Biol. Bull.* **175:** 361–371.

Mallet, A. L., C. E. A. Carver, S. S. Coffen, and K. R. Freeman. 1987. Winter growth of the blue mussel *Mytilus edulis* L.: importance of stock and site. *J. Exp. Mar. Biol. Ecol.* **108:** 217–228.

Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. *Quart. Rev. Biol.* **52:** 263–277.

Moore, W. S., and D. B. Buchanan. 1985. Stability of the Northern Flicker hybrid zone in historical times: implications for adaptive theory. *Evolution* **39:** 135–151.

Moore, W. S., and W. D. Koenig. 1986. Comparative reproductive success of yellow-shafted, red-shafted and hybrid flickers across a hybrid zone. *The Auk* **103:** 42–51.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43:** 223–225.

Richardson, C. A., D. J. Crisp, and N. W. Runham. 1979. Tidally deposited growth bands in the shell of the common cockle *Cerastoderma edule* (L.). *Malacologia* **18:** 277–290.

Roff, D. A. 1980. A motion for the retirement of the von Bertalanffy function. *Can. J. Fish. Aquat. Sci.* **37:** 127–129.

Sanjuan, A., H. Quesada, C. Zapata, and G. Alvarez. 1990. On the occurrence of *Mytilus galloprovincialis* Lmk. on the N.W. coast of the Iberian Peninsula. *J. Exp. Mar. Biol. Ecol.* **143:** 1–14.

SAS Institute. 1987. *SAS/STAT Guide for Personal Computers.* Release 6.03 ed. Cary, NC.

Seed, R. 1971. A physiological and biochemical approach to the taxonomy of *Mytilus edulis* L. and *Mytilus galloprovincialis* (Lmk.). *Cah. Biol. Mar.* **12:** 291–322.

Seed, R. 1972. Morphological variations in *Mytilus* from the French coasts in relation to the occurrence and distribution of *Mytilus galloprovincialis* (Lmk.). *Cah. Biol. Mar.* **13:** 357–384.

Seed, R. 1974. Morphological variations in *Mytilus* from the Irish coasts in relation to the occurrence and distribution of *Mytilus galloprovincialis* (Lmk.). *Cah. Biol. Mar.* **15:** 1–25.

Skibinski, D. O. F. 1983. Natural selection in hybrid mussel populations. Pp. 283–298 in *Protein Polymorphism: Adaptive and Taxonomic Significance*, G. S. Oxford and D. Rollinson, eds. Systematics Association Special Volume 24, Academic Press, London.

Skibinski, D. O. F., and J. A. Beardmore. 1979. A genetic study of intergradation between *Mytilus edulis* and *Mytilus galloprovincialis*. *Experientia* **35:** 1442–1444.

Skibinski, D. O. F., and E. E. Roderick. 1989. Heterozygosity and growth in transplanted mussels. *Mar. Biol.* **102:** 73–84.

Skibinski, D. O. F., and E. E. Roderick. 1991. Evidence of selective mortality in favour of the *Mytilus galloprovincialis* Lmk phenotype in British mussel populations. *Biol. J. Linn. Soc.* **42:** 351–366.

Skibinski, D. O. F., M. Ahmad, and J. A. Beardmore. 1978a. Genetic evidence for naturally occurring hybrids between *Mytilus edulis* and *Mytilus galloprovincialis*. *Evolution* **32:** 354–364.

Skibinski, D. O. F., J. A. Beardmore, and M. Ahmad. 1978b. Genetic aids to the study of closely related taxa of the genus *Mytilus*. Pp. 469–486 in *Marine Organisms. Genetics, Ecology and Evolution*, B. Battaglia and J. A. Beardmore, eds. Plenum Press, New York.

Skibinski, D. O. F., J. A. Beardmore, and T. F. Cross. 1983. Aspects of the population genetics of *Mytilus* (Mytilidae: Mollusca) in the British Isles. *Biol. J. Linn. Soc.* **19:** 137–183.

Sokal, R. R., and F. J. Rohlf. 1981. *Biometry.* 2nd ed. W. H. Freeman and Company, San Francisco.

Tracey, M. L., N. F. Bellet, and C. D. Gravem. 1975. Excess homozygosity and breeding population structure in the mussel *Mytilus californianus*. *Mar. Biol.* **32:** 303–311.

Willis, G. L., and D. O. F. Skibinski. 1992. Variation in strength of attachment to the substrate explains differential mortality in hybrid mussel (*Mytilus galloprovincialis* and *M. edulis*) populations. *Mar. Biol.* **112:** 403–408.

Yonge, C. M. 1949. *The Sea Shore.* Collins, New Naturalist Series, London.

Yonge, C. M., and J. I. Campbell. 1968. On the heteromyarian condition in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytiliacea. *Trans. R. Soc. Edinb.* **68:** 21–43.